THE ANATOMY AND PHYLOGENETIC POSITION OF THE BETULACEAE*

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According to the system of Engler the Betulaceae are placed together with the Fagaceae in the cohort Fagales, which in turn is assigned to a position near the bottom of the Archichlamydeae. At the beginning of the Archichlamydeae is found the cohort Verticillatae, containing but one family, the Casuarinaceae. The Casuarinaceae are represented by a single genus, Casuarina, and the species of the latter occur in the Australasian and East Indian regions.

In this work it is my purpose to treat anatomically and phylogenetically the family Betulaceae. First, however, in order better to understand the situation with regard to this family, it seems best to treat somewhat in detail the family Casuarinaceae which is in close anatomical and phylogenetic relationship with the above.

The position of these lower families, as has been stated, is the one given by Engler and generally followed. However, since the origin of the Angiosperms is still somewhat in doubt, opinions with regard to the true evolutionary position of the various lower members of the Dicotyledons naturally vary. Evidence for one view is favored by one organ while perhaps another may give just as convincing evidence for an opposite conclusion. It is only when everything is taken into consideration that one can arrive at a proper understanding of the true situation.

Among the various opinions there are two in particular which stand out from the others. The first is that of an origin from the Cycadales, while the second is one from the Coniferales through the Gnetales. Both of these views were based until recently almost exclusively upon the reproductive structures. Of late, however, Thompson (1912) has undertaken a study of the Gnetales with the vegetative anatomy as his object and has already published his results as found in the genus Ephedra. His research brings forward evidence

for the coniferous origin of the Angiosperms rather than for a deriva-
tion from the Cycadales. To quote directly from the author's pub-
lished account: "The idea of cycadalean and bennettitalean affinity
receives little support from the anatomy of Ephedra. On the other
hand, there are many points which are opposed to it and in favor of
the coniferous relationship; the arrangement of the primary vascular
bundles, double leaf-traces, arrangement and structure of the pits on
the tracheides, bars of Sanio, tertiary spirals, trabeculae and resin
plates, primitive uniseriate lignified rays, wood parenchyma, and
endarch vascular bundles of the leaf. The Gnetales do not appear to
have arisen from any modern group of Conifers, but rather from or
close to the base of the coniferous line."

"An angiospermous affinity is indicated by the possession of true
vessels, broad rays, and separation of the leaf-traces upon the stem."
Figure 1 shows a tangential view of the broad (aggregate) ray in
Ephedra californica.

Among others who have held to the idea of the gymnospermous
affinity of the Angiosperms we find Eichler (1878) stating that the
Amentiferae are derived directly from certain gymnospermous families.
Treub (1891) and others were also of this opinion.

The next question to arise is which of the families of the Angio-
sperms are lowest and hence most closely allied to the Gymnosperms.
Here again a diversity of opinion prevails. Eichler (1890), according
to the account of Moss (1912), considered Casuarina as belonging
to the amentiferous forms and as not having peculiarities striking
enough to warrant a separation from this group. Engler (1897)
himself so placed the genus until Treub's work appeared in 1891.
Treub claimed that certain reproductive characteristics made it neces-
sary to consider the Casuarinaceae as lower than the Amentiferae
proper. Since that time the family has been placed by Engler's
system in the Verticillatae at the very bottom of the Dicotyledons.
Warming (1912) justifies this position in the following words: "By
the transfusion tissue, by the type of the stomata, and especially the
ovular peculiarities, the order seems to be related to the Gymnosperms,
especially the Gnetales." With regard to the ovular peculiarities, he
found that "in the nucellus, which has two integuments, many embryo-
sacs are formed, of which only one is fertilized. The egg-apparatus
consists, as among the Angiosperms, of an egg-cell and two synergidae;
but antipodal cells are not formed. Before fertilization a prothallus of

many free nuclei is developed which after fertilization becomes a nutritive tissue. The fertilization is chalazogamic." These remarks according to Moss (1912) are based upon Treub's work. Moss, however, goes on to say that Frye (1903) has shown Treub to be wrong in regard to the anomalous embryo-sac, large number of nuclei, etc. He remarks that all of these characters suggested by Treub have been found in *Carpinus* and many of them in *Corylus, Betula* and *Alnus*. These are such as chalazogamy (fertilization of the egg-nucleus through the chalaza rather than direct as in the case of the majority of the Angiosperms), the occurrence of more than one embryo-sac, the formation of a coecum from the originally isodiametric embryo-sac, the occurrence of tracheides among the embryo-sacs, the entrance of the pollen tube at the base of the coecum in Corylus and Carpinus, the closure of the micropyle, and finally the fusion of the ovule with the wall of the ovary. Frye's results are corroborated by the work of Benson (1894), who showed that chalazogamy not only prevails among the Casuarinaceae but also among the Betulae and Coryleae, and that Castanea as well as Casuarina possesses tracheides around the base of the embryo-sac. Again, Benson (1906), in collaboration with Sanday and Berridge in 1906, found still further evidence that Casuarina differs in no essential from others of the Amentiferae. All genera, as she remarks, contain arborescent, wind-pollinated species. All are monoecious with flowers closely aggregated in unisexual catkins. The female flower in all is dimerous, bearing free stigmas, and the ovary of all genera is inserted in a radial plane. Casuarina differs from Carpinus exactly as does Quercus from Fagus, and the absence of a perianth in the female flower of Casuarina is a character common to Betula and Alnus. She states that the most important features of difference are its switch-like character and its phyllotaxy. These combined with some minor differences in floral structure and in embryology may suffice as grounds for forming a distinct group within the Betulaceae equivalent to the Coryleae. Thus he would dispense with the term Verticillatae and leave out such a cohort in the classification of the Dicotyledons.

From the above brief statement the reader may observe that the actual phylogenetic position of the Casuarinaceae remains at present somewhat in doubt. Although, as stated above, it is now placed in a cohort of its own at the very base of the Dicotyledons, yet there are recent data to show that it is really in no important respect distinct

from the Betulaceae and other amentiferous plants.   As will be noted, the work in this case, as well as in the case of the Gnetales, has been for the most part confined to the reproductive structures with no special reference to the vegetative bodies.   Let us now turn to a somewhat brief survey of the latter structures in Casuarina.   As work is now being carried on in this laboratory with regard to the above, it is not necessary to enter into a detailed discussion, but several points may be emphasized.

In studying the anatomy of a group of plants in order to determine their evolutionary relationships it is especially desirable to know and to be able to interpret their wood structure.   Recent work on the Gymnosperms has proved of great assistance and one is now able to classify them more nearly in a true phylogenetic order.   Little work has as yet been done upon the Angiosperms; but if the principles used in the case of the Gymnosperms are valid, they should hold equally in the case of the Angiosperms.

With this in mind we may turn to the anatomy of the Verticillatae. The wood, here, contains vessels which are small in diameter.   These have, even when in contact with the wood parenchyma, bordered pits.   Their end walls may often have simple, elliptical perforations such as are characteristic of the more highly developed Angiosperms, but these, in every case examined, are accompanied by the scalariform type characteristic of the lower forms.   In some species the vessels also have spiral tertiary thickenings.   Wood parenchyma is quite abundant and is always found scattered throughout the entire annual ring in the same position (diffuse) as it occurs in the higher Gymnosperms.   With regard to the wood prosenchyma the walls are usually thick and possess the bordered pits characteristic of Gymnosperms.

It is in connection with the rays that the most interesting condition is found.   Among the Coniferales the rays are uniseriate except in the case of those which contain horizontal resin canals.   This condition is not prevalent among the Dicotyledons, or even among the Gnetales, although some uniseriate rays are present.   Later it is my purpose to trace the evolutionary development of the higher types of rays but it will now be advantageous simply to state the situation as it exists in the Casuarinaceae.   Certain species, such as *Casuarina torulosa* (figure 2), show around the leaf-trace a congestion and grouping of the rays into a large, "false ray,"—the aggregate type.   This character persists throughout the entire growth of the plant.   In other forms a

different situation occurs. *Casuarina Fraseri*, for instance, shows in the primitive regions a ray quite like the type found throughout the wood of *Casuarina torulosa*. In maturity, the woody elements have been entirely lost and the small rays have become completely fused into an exceedingly large one. Such a ray is called compound. There is still another type, that found in *Casuarina equisetifolia* and *Casuarina stricta*. Here the rays in the first annual rings are in the aggregate stage. When the tree is old enough, a different condition from that found in *Casuarina Fraseri* occurs. The rays do not fuse together to form one large ray. Instead, as the aggregate type passes into the outer rings of growth, there is a tendency to separate, or, in other words, to become diffused into small rays two or three cells in width. If a large section is examined, this diffusion will be seen to take place in a perfectly diagrammatic manner. Thus Casuarina is a generalized type, as appears when one looks at the matter from the standpoint of the ray formation.

Turning from the Casuarinaceae let us consider the amentiferous forms in order to obtain some idea of the position which they occupy in the evolutionary scale. At present the Betulaceae and Fagaceae are placed in one cohort called the Fagales. This cohort is allocated by Engler eleventh from the base of the Dicotyledons. Since there is much uncertainty as to the exact relationship of these lower cohorts, the placing of the Fagales in the eleventh position simply means that the group belongs near the base of the Dicotyledons. Until recently the study of these forms, as in the case of the Casuarinaceae, has been confined largely to the reproductive organs. From such studies great diversity of opinion has arisen and no definite conclusions have been reached. In order that the reader may obtain some idea of the apparent confusion which has resulted, it seems desirable to give a brief account of the situation.

The peculiar floral apparatus, the ament, has caused much uncertainty upon the part of observers. A large group hold that the floral structure is not a primitive but a reduced form. Van Tieghem (1868), as far back as 1868, after making a study of Juglans (belonging to the cohort Juglandales) and of the Coryleae, claimed that their floral anatomy was similar to that of the higher Angiosperms. Prantl (1887), in his study of the Cupuliferae, looked upon the Fagaceae and the Betulaceae as derived by reduction from plants with bisexual flowers, possessing a perianth, multilocular ovary, and suspended

ovules. He considered that the two families have been developed independently, the Fagaceae being the more primitive of the two (a view not held by all). Hallier (1901 and 1908) attempted to demonstrate the affinity of the Cupuliferae and the higher Angiosperms. In doing so he considered the Cupuliferae as derived from the Hamamelidaceae and through these from the Laurineae. In this way he would connect them with the Rosalean forms allied to the Combretaceae. It is noteworthy in this connection that in 1908 he discarded the view held in his earlier paper and considered the above as derived from the Anacardiaceae and Burseraceae chiefly because of the strong anatomical likeness of Juliana to those orders upon the one hand and to Juglans upon the other. Clearly the observer had very small proof upon which to base his belief and hence, perhaps, his reason for changing his opinion. Goebel (1905), through his work, came to the conclusion that the Fagales and Juglandales are reduced forms. The superior gamophyllous perianth, syncarpous ovary, and complicated inflorescence, he thought not characteristic of a primitive family. Arber and Parkin (1907) also took issue with those who consider the same cohorts as not being reduced forms. Recently Berridge (1914) observed that the Amentiferae are not an isolated group but have an obv`ous relationship with the higher Angiosperms. In her article, the inflorescence, flowers and cupule, of *Castanopsis chrysophylla* are described and the anatomical structure of the flower is fully worked out. This species is compared to *Castanea vulgaris, Fagus sylvatica, Quercus Robur*, and *Juglans regia*. She found the flower differing in no essential from the epigynous types of the angiospermous flowers and drew a comparison between the Rosaceae and the Cupuliferae, since it seemed probable to her that the epigynous Rosaceae, or their near descendants, are the forms with closest affinity to the ancestors of the Fagaceae.

Among those who hold a different view upon the subject we find such men as Treub and Engler. Since those who believe in the reduction theory have worked freely with the Juglandales, it is well to note the work of other investigators upon the same group. Nawaschin and Finn (1913) worked with *Juglans regia* L. and *Juglans nigra* L. and came to the following conclusions: Among seed plants there is the tendency to reduce the male gametophytes from sperms to naked nuclei. Together with this reduction occurs the evolution of the pollen tube. The species of Juglans studied have binucleate genera-

tive cells which reach the embryo-sac without disorganization and which nearly correspond to the binucleate generative cells of certain Gymnosperms. In this feature, therefore, they conclude that these species occupy an intermediate position between the Gymnosperms, in which the male cytoplasm reaches the egg-cell, and the higher Angiosperms in which the male cytoplasm disorganizes in the pollen-tube and even in the pollen-grain. Hence they look upon the persistence of the male cytoplasm in Juglans as a primitive character retained from their gymnospermous ancestors; and, moreover, consider that the appearance of this character in chalazogams is significant and is a further proof of the great age of these plants. The tendency in seed plants to reduce the male gametes goes hand in hand with the evolution of the pollen-tube and seems correlated with its appearance. Such an opinion is the opposite of the one held by Van Tieghem (1868) in his work upon the floral anatomy of Juglans and the Coryleae. Nicoloff also (1904) came to an opposite conclusion from that of Van Tieghem and supported the views of Nawaschin. He considered the Betulaceae, as did Nawaschin, to be derived from the Coniferales while he would derive the Casuarinaceae from the Gnetales. Before discussing the above views let us note the opinion given by Coulter and Chamberlain (1903). Their position is one which does not bind them to either side. They state that none of the writers who regard the Amentiferae as derived from the Angiosperms with bisexual flowers suggest an affinity with any group of the Archichlamydeae but seem rather to incline to the author's opinion; namely, that whether they represent a single genetic stock or several, they appear to be isolated from the higher alliances.

By means of the short account just given in regard to the evolutionary position of the Fagaceae and the Betulaceae, one may readily understand that from the study of the reproductive structures alone the situation has not been well cleared up. Perhaps the position taken by Coulter and Chamberlain is the one which it is safest to assume when the above field alone is taken into consideration. However, some interesting facts may be pointed out from what has already been said concerning Casuarina. If, as appears to be the opinion of some, the Casuarinaceae are so closely allied to the amentiferous type of plants as to be almost, if not quite, worthy of being placed with them instead of in a group by themselves, then how can the latter group be considered as one which has undergone any great reduction?

To be sure there may be indications of reduction in some instances with regard to the reproductive structures, but on the other hand, such investigators as Nawaschin have found good grounds for supposing that there are very important primitive features in connection with the formation of the male cell which lead to a very different conclusion. That Juglans should show a condition part way between the Gymnosperms and the higher Angiosperms would appear to constitute a strong point against the contention that any great reduction has taken place. Moreover, the vegetative anatomy of the Casuarinaceae is most certainly primitive. Nearly every organ in this family shows primitive features although they are sometimes accompanied by characters common to the higher forms. Granting the close relationship to the Casuarinaceae it does not seem possible to regard these amentiferous forms as belonging anywhere but low in the evolutionary scale of the Dicotyledons. There are, also, other points which are, perhaps, best mentioned here. The species of all these families are characterized by having the egg fertilized from the lower side through the chalaza. Such a type of fertilization, as has been stated, is commonly known as chalazogamy in contrast to the type found throughout all the Monocotyledons and higher Dicotyledons. This latter type is called porogamy. In the latter, also, the pollen-tube grows down the style of the pistil and instead of following the wall of the ovary, as in the case of the chalazogamous forms, grows directly through the intervening space and into the egg-sac by way of the micropyle. The chalazogamous type is confined, among the Dicotyledons, to the amentiferous forms in general and is plainly not of high evolutionary character. We find an instance of a similar condition among the Gymnosperms in the Araucarineae. Here, in the case of the genus Araucaria, the pollen falls upon the ligule. It does not grow directly down to the micropyle but follows the tissues of the ligule and scale until it attains a position immediately below the ovule. Upon arriving at this point, it grows straight upward through the lower side of the megasporangium and reaches the egg from the bottom. In the chalazogams the pollen falls upon the stigma and the pollen tube grows down through the solid tissue into the egg. Apparently the situation in those members of the Dicotyledons characterized by chalazogamy is intermediate between the case in the Gymnosperms and that in the higher Angiosperms. The grains of pollen no longer fall upon the ovule but the condition has not yet been reached

where they grow through space and thus fertilize the egg by way of the micropyle.

Another feature worthy of mention is the way in which these plants are pollinated. Among the Dicotyledons there are two chief agencies for carrying this out. All of the higher members of the group are pollinated by insects. Such plants usually possess well developed floral envelopes. On the other hand the Betulaceae, Fagaceae, and Casuarinaceae together with other families of the lower Dicotyledons and all of the Gymnosperms are not pollinated in this way. Pollination in these takes place through the agency of the wind. This has long been recognized as a characteristic common to the lower families of the Angiosperms. If these forms are reduced to any great extent, they would be expected to show some trace of insect pollination. An instance may be mentioned of a family which is even now placed very low because of its apparently simple floral structure but which is pollinated by insects. This family is that of the Salicaceae belonging to the cohort Salicales. Miss Holden (1912) has worked with these and, since the principles which she has used are the same as those which are being used here, it will not be amiss to give in some detail a summary of her results. Through recent work it has been shown that the presence of wood parenchyma and its distribution are very definite things and hence of great value in determining the evolutionary relationships of a plant. In the lowest Gymnosperms no wood parenchyma is present. When it first occurs, it appears only at the end of the annual ring (terminal) and is evidently developed in correlation to the alternation between summer and winter in connection with storage of food material. The next step, and one which is common to the higher Gymnosperms and the lower Angiosperms, is the diffusion of the wood parenchyma throughout the entire annual ring. Among the higher Angiosperms the wood parenchyma is more or less localized around the vessels. In Salix the parenchyma is terminal. This condition by itself is deceptive, since not even the higher Gymnosperms are so characterized. Again the rays throughout our common species of Salicaceae tend to be uniseriate like those of the Conifers. Because of this structure and by reason of the apparently simple flower this family has been placed at or near the bottom of the Dicotyledons.

Miss Holden in making her study used exactly the same principles which have led to such excellent results among the Gymnosperms.

These may be catalogued under three heads—recapitulation, retention, and reversion. The principle of recapitulation is of much importance in the case of plants. Very often the seedling gives evidence of an ancestral condition which no longer prevails in the mature form. The principle of retention, similar to that of recapitulation, is particularly characteristic of plants. Scott first brought this to light in connection with the peduncle of the Cycads. More recently this principle has been greatly extended and it is now known that certain organs and regions of the plant often retain ancestral conditions lost in the more advanced parts. Thus the root throughout all plants is characterized by centripetally developed primary wood which now does not appear in the stem of any forms above the zoidogamous Gymnosperms. Other parts which often manifest retention are the reproductive axis, the first annual ring of the vegetative or reproductive stem, the leaves, etc. The last principle, that of reversion, has been shown of late to be likewise of great importance. In this way conditions which are no longer present in our living forms may be recalled as a consequence of injury. In the consideration of the Betulaceae the validity of the general principles cited above will be assumed.

Of the two families classified by Engler in the cohort Fagales, the Fagaceae are generally thought to be the higher. This family consists of several well known genera, among which may be mentioned Quercus, Fagus, Castanea, and Castanopsis; and some of the anatomical peculiarities of these are here described. The genus Fagus is usually divided into two sections, namely, Eufagus and Nothofagus. The species of Eufagus (northern beeches) possess broad rays, while those of Nothofagus (antarctic beeches) have rays of only one to two cells in width. In addition to the distinctions of ray structure the wood fibers of Eufagus have bordered pits in contrast to those of Nothofagus in which the pits are simple. In the latter also the fibers are sometimes septate. Castanea and Castanopsis show close agreement with regard to the wood. Narrow medullary rays occur extending outward from the angular pith. A feature of difference from the two genera last named is the presence in Quercus of *broad* medullary rays.

The second family of the cohort Fagales and the one dealt with especially in this work is the family Betulaceae. It includes the following genera: Alnus, Corylus, Carpinus, Ostrya and Betula. In the anatomy of their woods certain general features occur. Narrow

medullary rays are present which are but one or two, rarely four, cells in width, the cells being mostly elongated in the radial direction and containing clustered crystals. The vessels have small lumina, are arranged in radial rows, bear bordered pits in contact with the ray parenchyma and always have scalariform perforations. Wood parenchyma is present and is not usually arranged in the plates so characteristic of Quercus. The wood prosenchyma or tracheids have wide lumina and bordered pits, which are not numerous and whose border is distinctly smaller than the pit itself. The above statements apply to the members of the Betulae (Alnus and Betula). Among the Coryleae (Carpinus, Ostrya and Corylus) there are many features in agreement with the Betulae. The medullary rays are small, usually being from one to two, or sometimes three, cells in width. The wood prosenchyma is characterized by wide lumina and bordered pits; and the vessels are always arranged radially with small lumina. However, where two vessels join each other, the walls bear densely packed and rather large bordered pits, the margin often assuming a hexagonal contour. Again, where the vessels come in contact with the ray parenchyma, their pits are almost entirely simple. There are spiral thickenings in some members. In all investigated species of Carpinus and Ostrya the perforations of the vessels are, for the most part, simple and elliptical, and the scalariform type is confined largely to the primary wood. Corylus, however, does have exclusively the scalariform type. The Coryleae in general have more wood parenchyma developed than do the Betulae and it is often found in bands as is characteristic of Quercus.

The preceding paragraph will afford an idea of the main features of the Betulaceae from the standpoint of wood structure. It is chiefly from the evolutionary aspect that they will be treated in this work. From this point of view, as in the case of the oaks, the rays show very interesting and important conditions.

Alnus, a genus ranging in stature from the arboreal to the fruticose, is generally distributed throughout the north temperate zone, and is abundant in eastern North America and in eastern Asia. Its rays vary much in size and degree of development according to the species. Bailey (1912) has already shown this in some detail. So far as his work goes, it has been possible to verify his results. Certain forms, as *Alnus acuminata*, show practically no tendency towards aggregation of the ray. Instead, the rays, even in the mature stem, are usually

uniseriate. This is not a feature characteristic of the whole group; but is rather the exception. Take, for example, our common form, *Alnus incana* L. Here the entirely uniseriate rays contrast with apparent aggregations of rays. In the latter the slender component rays are separated from one another by fibers only; the vessels characteristic of the remaining wood structure being conspicuous by their absence. *Alnus rugosa* Du Roi shows a condition very similar to that of *Alnus incana* and therefore needs no special description.

In the case of *Alnus japonica* a somewhat different situation is present. In figure 3 is shown part of the woody cylinder of a three-year-old branch of this species. Vertically in the center is seen the aggregation of rays corresponding to a leaf-trace, terminated below by the trace itself and subtending the leaf-gap. In the aggregation of rays, vessels are clearly absent. On either side of this central congery of rays lies the wood which has the ordinary structure except where smaller aggregate rays are present. The latter are the dwindling remnants of foliar aggregations belonging to nodes higher or lower in the stem.

Figure 4 is a tangential view under about the same magnification, taken from the stem of the same species. In the center near the top may be seen the round cluster of cells which makes up the leaf-trace and which pass out horizontally to the axis of the tree. Extending for a short distance above this and for a much greater distance below, a noticeably larger clustering of elements may be observed, differing from the surrounding tissue by the absence of vessels. Careful examination shows it to consist of groups of rays (one to three cells in diameter) and separated by tracheids only. In other words, it is an aggregate ray formed about the leaf-trace for the more abundant storage of food.

Various other alders show this tendency to aggregate still further carried out. In *Alnus rubra* the condition is quite like that of *Alnus japonica* with the rays gathered together and becoming more or less multiseriate. Still further compounding appears in *Alnus maritima* Marsh. It may be inferred from the above description that the alders illustrate as regards ray organization a relatively low condition.

Interesting situations are presented by *Alnus mollis* Fernald, a species of northern range commonly found throughout eastern Canada and the Eastern States, and only reaching southward along certain streams which have brought the seeds down in their current. In these southern limits of distribution, the species is much smaller in size than

when found in its natural habitat. Figure 5 shows a transverse section of the center of a twig in the region of the node. In the first annual ring a leaf-trace appears on the right with which is associated a vestigial aggregate ray.

This species affords an excellent example of retention and of recapitulation. The large rays, which have disappeared in the ordinary wood, appear again in the first annual ring at the node and around the leaf-traces. Figure 6, a transverse section of the wood of an old stem, shows that even in maturity it does not manifest aggregate rays. Wounding, as illustrated in figure 7, brings about a different situation. In the center several clustered rays occur, though in the regions lateral to these the ray structures are all uniseriate. In figure 8, a transverse section of a mature root, several aggregate rays appear in the outer rings and two such rays run completely through the field.

In the study of this species several salient facts may be noted. In the first place, in the normal stem the region of the internode does not normally show aggregate rays. When it is cut in the region of the node, aggregate rays appear to some extent within the first annual ring and around the leaf-traces. An examination of the seedling root shows its rays to be all uniseriate. Yet, around the root-trace and somewhat after wounding, the aggregate ray reappears, and in the old root it is a permanent feature.

Apparently *Alnus mollis* is a peculiar type, which, after starting to form aggregate rays, has reverted to the uniseriate condition. It is a well known fact that plants in a state of reduction often have ancestral structures in the mature parts. Thus, although the root of the seedling exhibits no large rays, since they have reverted to the uniseriate condition, in the root of the mature plant the aggregate ray reappears. The stem manifests a similar situation. The peduncle of the ovuliferous ament often presents aggregate rays in considerable numbers. The same condition is illustrated by the axes which support the peduncles, and, in fact, not infrequently in the early annual rings of any branches of vigorous development.

Figure 9 is an illustration of the first few annual rings of a twig of *Alnus Yasha*, a Japanese species. Here again, although the mature stem shows no large rays, yet, as the section indicates, in the first annual ring and around the leaf-traces aggregate rays make their appearance. Obviously the species has suffered degeneracy in a degree somewhat similar to that of *Alnus mollis*.

The genus Corylus is characterized by having aggregate rays throughout the entire stem. Figure 10 is a section of the root of *Corylus americana* Walt. cut through the region of the root-trace. It will be not ced that around the trace the rays are aggregated. Figure 11 is that of a longitudinal section of *Corylus rostrata* Ait. taken just below the root-trace. Only ray cells and tracheids with wood parenchyma cells appear extending through the center. It is the aggregate type which is formed about the leaf-trace or the root-trace. The genus Corylus is thus characterized by having the aggregate type of ray well developed in both root and stem.

In the genus Carpinus the situation is comparable to that of Corylus. Figure 12 is that of a transverse section of *Carpinus cordata* cut near the region of the leaf-trace. The rays are here clustered into more or less definite congeries in which the vessels are very scarce. In other words, the wood normally has rays in the aggregate condition. In figure 13, a transverse view of the root of the same species, the rays are in general diffuse but aggregated in relation to the root-trace. Figure 14 is a greater magnification of a portion of figure 13 showing more distinctly the area directly around the root-trace and better illustrating the same characteristics.

In the case of Ostrya the normal stem does not have the rays distinctly aggregated, but instead they are more or less scattered. Nevertheless, as figure 15 indicates, the aggregate condition is somewhat clearly shown in regions near the pith. This is another example of the retention of ancestral characters in the first annual ring. Figure 16, a transverse section of a root of *Ostrya virginiana* Mill., illustrates aggregation (bottom of the figure) and absence of this phenomenon in the rest of the periphery. Figure 17, a higher magnification of the lower part of the preceding photograph, shows the aggregate ray developed in relation to a secondary root. Here may be seen manifested the characteristics of aggregation; namely, the clustering of rays with the exclusion of vessels. The root, most conservative of plant organs, naturally reproduces the primitive condition, aggregation of rays in the vicinity of the appendages. In the stem, contrariwise, we have to do with the most progressive and variable of organs and as a consequence we are not surprised to discover the absence of aggregate rays in its mature structure. Vestiges of these, however, occur, as shown in figure 15, in the earlier annual rings and nearer the pith. In other words, the stem of *Ostrya virginiana* has passed through the

aggregate condition and is now characterized by the possession of the diffused type of ray in its mature organization.

In the case of the Betulae there are extremely interesting facts. In *Betula populifolia* Marsh. aggregate rays are characteristically present more or less throughout the whole plant. Because it has the aggregate ray present everywhere, this species must be regarded as one of the most primitive of the birches. On the other hand, *Betula lenta* L., the black or cherry birch, appears to represent a higher degree of development; for in the normal stem aggregation is conspicuously absent. Figure 18 shows a transverse section of *Betula lenta* cut through the root near the root-trace. The two aggregate rays may be plainly seen clustered about the region of the outgoing traces. Again it will be noted that the root illustrates the retention of the ancestral characters of the plant. The European white birch, *Betula alba* L., and its variety the canoe birch, *Betula alba* var. *papyrifera* Marsh., likewise supply interesting data. Figure 19 is that of a transverse section of the stem of *Betula alba* cut from a small twig at the very top of the tree. In the center of the field a very noticeable and large aggregate ray is visible. Such rays are characteristic of the vigorous upper catkin-bearing branches of this species. Ancestral structures are well known to occur in reproductive regions; and the situation presented by the species under consideration affords a further illustration of this important general principle.

Figure 20 shows a transverse section of a seedling twig of *Betula alba*, var. *papyrifera*. It has been wounded at about the third annual ring and again near the end of the fifth year. As a result of the wounds the structure has reverted and has formed many large aggregate rays. This is another instance of the traumatic recall of ancestral types, a condition very common throughout the Conifers. Figure 21 shows a small portion of figure 20 enlarged. It is clear that the majority of the rays are from two to three cells in width, *i. e.*, of the diffused type. Upon either side, however, is a large aggregate ray which has come in subsequent to the wounds shown in figure 20.

Figure 22 is that of a young twig of the same species cut in the vicinity of the leaf-trace. In the normal stem cut from the internode no large rays appeared. Nevertheless, around the lateral leaf-traces a tendency to aggregate occurs in the first annual ring and somewhat in the second, but beyond these only the diffused type is present. Figure 23 is a transverse section of a twig cut from the extreme top of an old

and vigorous tree and illustrating a condition similar to that shown in figure 19. Aggregate rays are not noticeable in the mature vegetative stem of this species except in relation to the leaf-trace and in the first annual ring. They are conspicuously present for a number of years in the seedling stem of *Betula alba* (*sensu strictiore*), but are not found even in the first annual ring of the seedling of *B. alba*, var. *papyrifera*. The *wounded* seedling of the variety does, however, show aggregate rays strongly developed as a result of injury. The vigorous catkin-bearing branches of this species likewise often manifest the aggregate ray clearly present, and figure 24 illustrates the interesting conditions which are found in the root. On the upper side of the figure appears a denser region of the wood increasing in breadth from the primary wood outwards. This is an aggregation of rays related to the trace of an outgoing secondary root.

CONCLUSIONS

On the whole the genus Alnus most clearly illustrates the conditions which are apparently primitive for the Betulaceae. In *Alnus japonica*, for example, we find congeries of somewhat enlarged rays related to the appendages (roots, leaves and lateral branches). These clusters of rays present in several features a contrast to the general ray conditions in the wood. First of all, the members of such ray groups are individually lengthened or broadened or both in contrast to the uniseriate organization of the rays of the mass of the wood. Secondly, they show more or less pronounced tendency to fuse with one another. Thirdly, the vessels which characterize the longitudinal structure of the normal wood are conspicuous by their absence in the grouping of rays under discussion. This condition of organization is well illustrated by *Alnus japonica* as figured in plate I. In other species of *Alnus* the tendency to grouping or aggregation of rays with the concomitant peculiarities described above becomes obsolescent, being retained only in regions of greater conservatism and susceptible to recall as a result of injury. *Alnus mollis*, *Alnus rugosa*, *Alnus incana*, *Alnus maritima*, etc., etc., show more or less marked degeneracy in these particulars.

In the genus Corylus the condition is simple. As figures 10 and 11 indicate, there is a distinct tendency towards aggregation.

In the genus Carpinus we apparently have a very interesting situation. Here in most species the wood structure is characterized

by rays not uniseriate as in Alnus, but two or three cells wide and separated from one another by the usual longitudinal elements, namely, vessels, fibers and wood parenchyma cells.   In contrast to this organization of the wood which may be justly considered to be normal, we find clustered rays not opposed as in *Alnus* to those of the general wood structure but distinct because of their clustered condition as well as by reason of the absence among them of the longitudinal elements belonging to the category of vessels.   It has been made clear at the beginning of this article in connection with the genus Casuarina that the type of dicotyledonous wood characterized by the uniform distribution of rays not uniseriate but usually of mediocre breadth (two to many cells) is the result of the diffusion of rays originally grouped, throughout the woody cylinder.   The special interest of Carpinus is that it presents this condition and that of aggregation from which it has been derived, side by side.   In *Carpinus cordata* aggregate rays are found only in the earlier annual rings, disappearing in the adult.   On the other hand, in *Carpinus caroliniana* and *Carpinus betulus* the aggregate and diffuse ray conditions persist together in the mature structure.

The wood organization of Ostrya is very similar to that of *Carpinus cordata*.   In the mature wood of the stem grouped rays have entirely disappeared, but vestiges of them may be discerned in the earlier annual rings adjacent to the pith.   The aggregate rays also persist in this genus in the root.

The genus Betula is of peculiar interest on account of the large number of species and the considerable variety of wood structure which they present.   In the common gray birch, *Betula populifolia*, of the Eastern States, we find diffuse rays and aggregations of rays close together.   In *Betula alba* the congeries or aggregations of rays are found in the first annual ring of the vegetative stem, during a number of years in the seedling stem, and even more strikingly in vigorous reproductive branches.   Aggregations of rays are likewise a feature of normal structure in the root and are related to the secondary roots. In *Betula papyrifera* (*Betula alba*, var. *papyrifera*) the occurrence of aggregations of rays is much more restricted.   They are absent in the seedling, but are normally found in the root.   They may be recalled in the seedling stem though not in the adult as a consequence of injury. In *Betula lenta* and *Betula lutea* the condition of aggregation is clearly present only in the root.   It is thus apparent from this summary

that in the genus Betula the phenomenon of aggregation of rays is a primitive condition persisting with the diffuse type in *Betula populifolia*, but in other species confined more or less definitely to primitive organs and regions or recalled only as a result of injury.

In a recent article an attempt has been made to discredit the aggregate ray as the precursor of the conditions of ray structure obtaining in the mass of arboreal Dicotyledons (Bailey and Sinnott, 1914). In the present connection it can only be emphasized that the conclusions which are logically drawn from the facts must be in accord with the general principles established as a result of the comparison of fossil (Mesozoic and Paleozoic) Gymnosperms with those still living. It is certain from these studies that ancestral conditions persist strongly in reproductive structures and in roots, and that they may be present in the earlier rings of growth of the vegetative stem even when absent in the mature wood. Further, they often reappear in response to injury or abnormal situations. Applying these principles to the Betulaceae from Alnus to Betula, beyond reasonable question the phenomenon of aggregation of rays is primitive for the family. The genus Alnus illustrates this type in a primitive condition. In the higher genera, Carpinus, Ostrya and Betula, it has given place to the diffuse state resulting from the lateral spreading of the original congeries or aggregations of rays; but in these genera the ancestral condition often persists in conservative organs and regions or may return as a consequence of injury. If the principles here cited are sound and the conclusions drawn are logical, the criticism above referred to appears to have very slight value.

It seems clear that the anatomy of the cohort, of which the Betulaceae form one member, is distinctly that of a low group. The presence of parenchyma distributed throughout the entire annual ring is a feature not usually found in the higher Dicotyledons. The vessels, also, with their characteristically scalariform perforations are unquestionably of a primitive nature. The fibers are in general fiber-tracheids, and above all, the rays show features of organization which are common to the lower families of Angiosperms and to the highest Gymnosperms. With these facts in view, it is obviously impossible to assign this family to a very high position.

SUMMARY

1. That, although the floral anatomy of the Betulaceae may give indications of a reduction instead of primitiveness, yet there are other facts which must be taken into consideration.

2. That whether the Verticillatae should or should not be separated from the Amentiferae is not a question of great importance from our standpoint.

3. That the structure of the Verticillatae is either entirely primitive or so generalized as to include both primitive and advanced conditions, thus indicating that the cohort belongs close to the base of the dicotyledonous line.

4. That the closeness of anatomical relationship between the Verticillatae and the true Amentiferae gives evidence as to the primitiveness of the latter.

5. That the Betulaceae in general show clear evidence of a primitive aggregation of specialized rays in relation to the appendages, and that these rays become subsequently diffused throughout the structure of the wood.

6. That the alders in general present the aggregate condition either normally developed or in a state of reduction.

7. That in the higher members of the Betulaceae (Carpinus, Ostrya and Betula) the aggregate condition clearly lies in the evolutionary background, persisting only in conservative organs and regions or recalled by injuries.

8. That the general internal anatomy of the Betulaceae and especially the ray structures supply no proof for and much against their being placed anywhere but near the base of the Dicotyledons.

9. That, finally, unless some new and more conclusive facts to the contrary are brought to light, the Betulaceae must be ranked in a low phylogenetic position.

In conclusion, the writer wishes to express his thanks to the authorities of the Arnold Arboretum for the privilege of collecting material with which to carry on this work; and, also, to those who have in any way aided.   This work has been done in the Phanerogamic Laboratories of Harvard University under the direction of Prof. E. C. Jeffrey.

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EXPLANATION OF PLATES XVI–XIX

FIG. 1. *Ephedra californica.* Tangential section of wood showing aggregate ray. × 30.

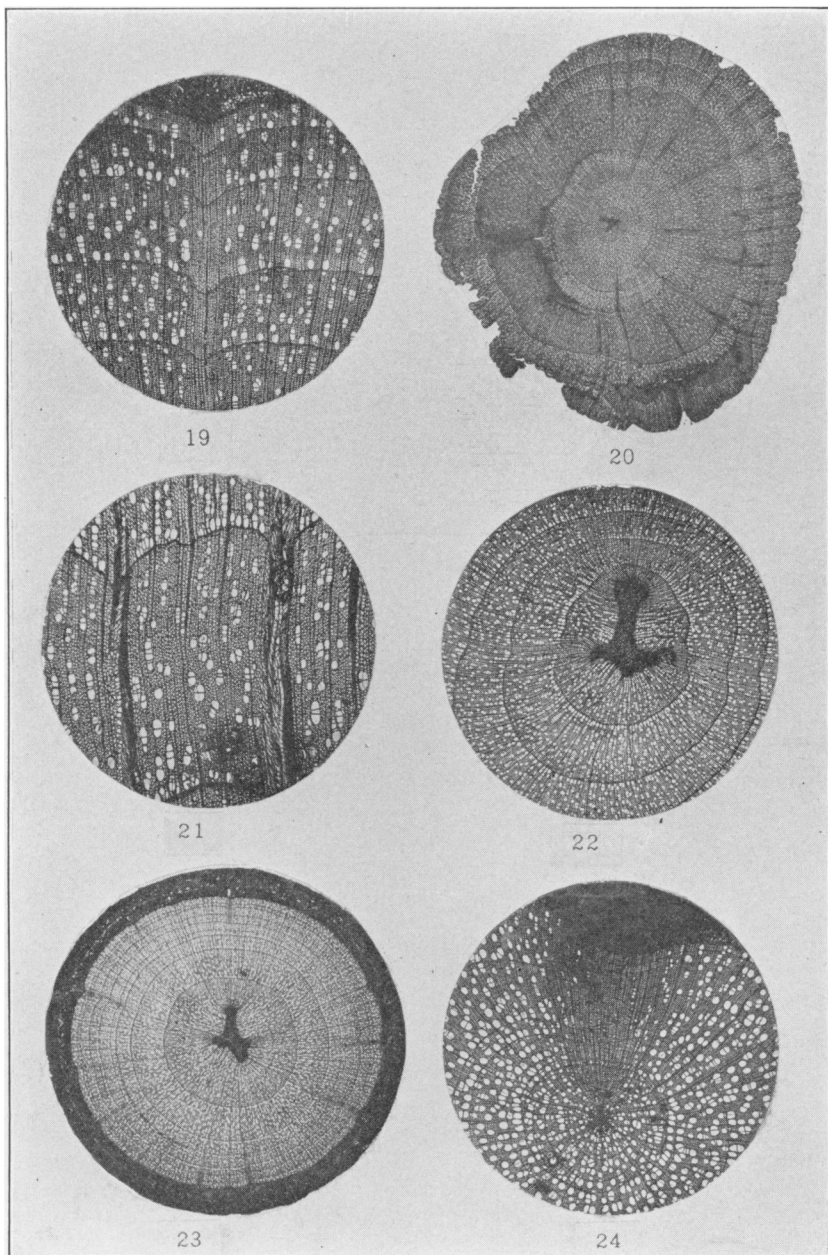HOAR: ANATOMY OF BETULACEAE.

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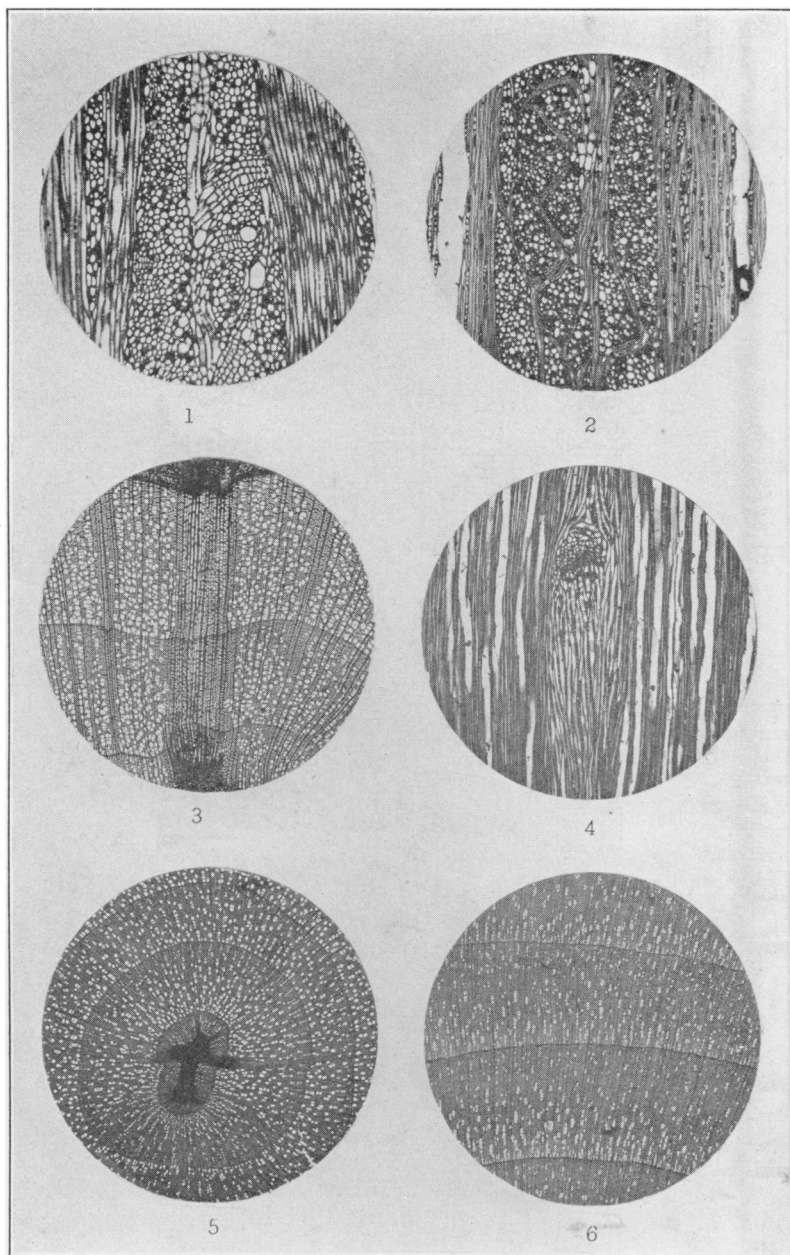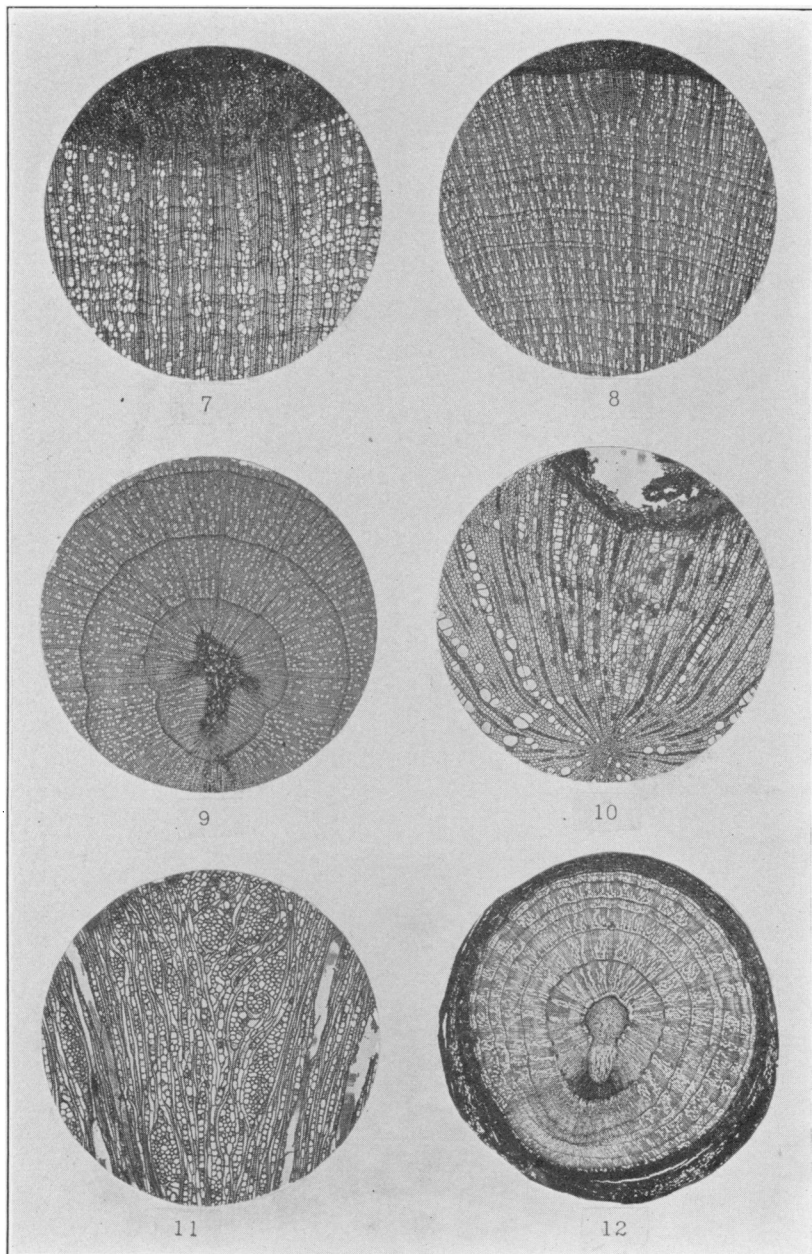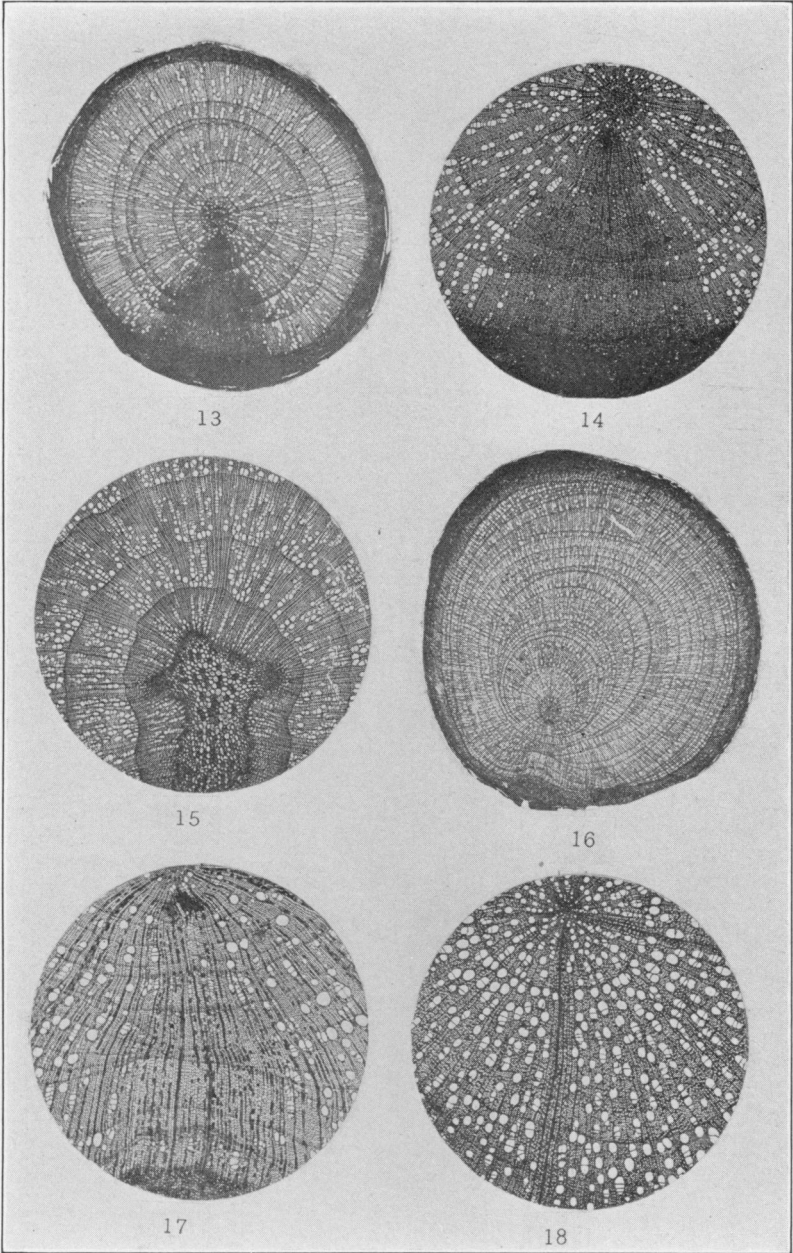
FIG. 2.   *Casuarina torulosa.* Tangential section of wood showing aggregate ray.   × 30.

FIG. 3.   *Alnus japonica.* Transverse section of aggregate ray enlarged in vicinity of leaf-trace.   × 20.

FIG. 4.   *Alnus japonica.* Tangential section through aggregate ray and leaf-trace.   × 25.

FIG. 5.   *Alnus mollis.* Transverse section of young twig through region of node showing aggregate rays, the largest of which is related to a leaf-trace.   × 10.

FIG. 6.   *Alnus mollis.* Transverse section of wood of stem showing only uniseriate rays.   × 20.

FIG. 7.   *Alnus mollis.* Transverse section of wounded root showing aggregations of rays.   × 20.

FIG. 8.   *Alnus mollis.* Transverse section of part of an old root showing normal aggregate rays.   × 15.

FIG. 9.   *Alnus Yasha.* Transverse section through the first annual ring of a twig showing aggregations of rays.   × 15.

FIG. 10.   *Corylus americana.* Transverse section in the region of a root-trace showing aggregation of rays in relation to the lateral root.   × 25.

FIG. 11.   *Corylus rostrata.* Tangential section cut in the vicinity of the root-trace showing aggregation of rays.   × 25.

FIG. 12.   *Carpinus cordata.* Transverse section of twig showing aggregations of rays.   × 10.

FIG. 13.   *Carpinus cordata.* Transverse section of root showing an aggregate ray related to a secondary root.   × 15.

FIG. 14.   *Carpinus cordata.* Transverse section of the same aggregate ray as in Fig. 13 enlarged.   × 30.

FIG. 15.   *Ostrya virginiana.* Transverse section through the early annual rings showing a persistent tendency to aggregate.   × 20.

FIG. 16.   *Ostrya virginiana.* Transverse section of root showing aggregation of rays about the trace of lateral root.   (Upper side).   × 15.

FIG. 17.   *Ostrya virginiana.* Transverse section of aggregate ray around trace of lateral root, much enlarged.   × 30.

FIG. 18.   *Betula lenta.* Transverse section of root showing aggregation of rays in relation to lateral roots.   × 30.

FIG. 19.   *Betula alba.* Transverse section of wood of a twig near the top of the tree showing aggregation of rays.   × 20.

FIG. 20.   *Betula alba* var. *papyrifera.* Transverse section of axis of wounded seedling showing traumatic aggregate rays.   × 15.

FIG. 21.   *Betula alba,* var. *papyrifera.* Part of Fig. 20, more highly magnified.   × 30.

FIG. 22.   *Betula alba,* var. *papyrifera.* Transverse section of twig in region of node showing vestigial aggregations related to leaf-traces.   × 10.

FIG. 23.   *Betula alba,* var. *papyrifera.* Transverse section through reproductive branch showing persistence of aggregate rays.   × 10.

FIG. 24.   *Betula alba,* var. *papyrifera.* Transverse section of root showing aggregate ray related to lateral root.   × 15.